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OSTEOLOGY OF POLYGLYPHANODON, AN UPPER  
CRETACEOUS LIZARD FROM UTAH

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ONE of the important discoveries made by the 1937 Smithsonian paleontological expedition to central Utah was the finding of eight individuals of an undescribed member of the Sauria. In 1938 a field party under Dr. C. L. Gazin revisited the locality and recovered the remains of four more individuals, one of which is the most complete skeleton yet found. These specimens, four of which were partially articulated, so fully supplement one another that, except for the distal end of the tail, practically all other parts of the skeletal structure are now known. Although among the most ancient Sauria from North America, they have the distinction of being more completely preserved than any specimens of the suborder yet discovered on this continent. These specimens display a type of dentition not before known in the Sauria, either living or extinct.

Associated with the relatively abundant species is one other smaller species represented by several incomplete jaws.

A preliminary description of these two lizards has already been published,<sup>1</sup> and it is the purpose of the present paper to describe the complete osteology of *Polyglyphanodon*. The smaller forms of this fauna will be considered in a separate article.

The drawings illustrating this paper were made by Sydney Prentice.

<sup>1</sup> Gilmore, C. W., New fossil lizards from the Upper Cretaceous of Utah. Smithsonian Misc. Coll., vol. 99, No. 16, pp. 1-3, 1940.

## Order SAURIA

## POLYGLYPHANODONTIDAE, new family

For family relationships, see page 264.

## Genus POLYGLYPHANODON Gilmore

*Polyglyphanodon* GILMORE, Smithsonian Misc. Coll., vol. 99, pp. 1-2, 1940.

*Etymology*: *πολύς*, many; *γλύφᾶνος*, chisel; *ὄδους*, tooth.

*Genotype*.—*Polyglyphanodon sternbergi* Gilmore.

*Diagnosis*: Dentition subacrodont, heterodont; teeth posterior to the first seven transversely widened, with sharp transverse cutting edges; upper and lower teeth indistinguishable; skull deep, strongly constructed; pineal foramen on parietofrontal suture; premaxillary with long spine; postfrontal distinct; postorbital present, maxillary deep; squamosal wide dorsoventrally; coronoid extending high above level of ramus; splenial extensive but falling short of symphysis; surangular and articular distinct; angular greatly restricted on external surface; vertebrae procoelous; zygosplene and zygantrium well developed; centra tapering; 29 presacral, 2 sacral vertebrae; coracoid with one emargination; clavicles perforate; interclavicle anchor-shaped, with bifurcated proximal end; ilium with rectangular upper extremity; ischia and pubes like *Iguana*; limb bones of moderate length, stout; feet typically lacertian; digital formula of manus: 2, 3, 4, 5, 3; digital formula of pes: 2, 3, 4, 5, 4.

## POLYGLYPHANODON STERNBERGI Gilmore

*Polyglyphanodon sternbergi* GILMORE, Smithsonian Misc. Coll., vol. 99, pp. 1-2, fig. 1, 1940.

*Type*.—U.S.N.M. No. 15477, consists of the skull, lower jaw, and many skeletal parts; collected July 22, 1937.

*Paratype*.—U.S.N.M. No. 15816, consists of a nearly complete articulated skeleton; collected in July 1938.

*Locality*.—"South Dragon," Manti National Forest, Emery County, Utah.

*Horizon*.—Lower part of North Horn formation, Upper Cretaceous.

*Specific name*.—In honor of George F. Sternberg, who found the first specimen.

*Other specimens*: In addition to the type specimen there were skeletal parts of 11 other individuals available for this study. All of these came from a small "badland" area in a valley locally known as the "South Dragon," about midway between Ferron Canyon on the south and the road crossing the valley to North Horn Mountain on the north. There has been much faulting in this area, and I was

unable to determine the exact position of the lizard-bearing stratum in the Upper Cretaceous section. That it was in the dinosaur-bearing part of the section was abundantly indicated by the finding of several fragmentary dinosaur specimens both above and below the lizard layer. The locality is referred to at various places in this paper as the "lizard locality." (Pl. 24.)

A detailed list of the parts comprising the several specimens is here given in order that the reader may have a full knowledge of the available materials.<sup>2</sup>

## LIST OF AVAILABLE SPECIMENS

- U.S.N.M. No. 15477, type. Nearly complete skull and lower jaws with full dentition; axis and 3 articulated cervical vertebrae; 15 dorsal, 2 sacral, and 3 caudal vertebrae; complete pelvis; both femora; right tibia, distal end of left tibia; fibula, astragalus, calcaneum; many bones of hind foot and tarsus; humerus, lacking distal end; proximal end of ulna; numerous bones of fore foot; fifth cervical rib, right side; last thoracic rib of right side; many incomplete thoracic ribs. Collected by George B. Pearce, July 22, 1937.
- U.S.N.M. No. 15559: Left maxillary with teeth, articulated parietal and frontal, right quadrate, right ramus complete and part of left ramus, both with teeth, and skull fragments; 15 presacral vertebrae; right scapula and coracoid, part of left scapula; left clavicle; interclavicle; left humerus and distal half of right humerus; both ulnae; both radii; some carpal and fore-foot bones; fragmentary portions of pelvis; femur lacking proximal end; tibia; numerous pieces of ribs. Collected by George B. Pearce, July 22, 1937.
- U.S.N.M. No. 15566: Left quadrate with articulated squamosal; articulated series of 29 vertebrae (6C, 19D, 2S, 2Ca), greater portion of right scapula and coracoid; right clavicle complete and part of left clavicle; interclavicle; complete left humerus and fragments of right; both ulnae; radius; part of carpus and fore foot; nearly complete left half of pelvis and part of right half; both femora; both tibiae; many tarsal and bones of hind feet, most of the ribs of left side articulated, a few parts of ribs. Collected by George B. Pearce, July 22, 1937.
- U.S.N.M. No. 15567: 5 presacral vertebrae, incomplete tibia, and many fragmentary bones. Collected by George B. Pearce, July 22, 1937.
- U.S.N.M. No. 15568: Nearly complete disarticulated skull, both rami, good dentition; axis centrum, 3 cervical vertebrae; 6 dorsal and 22 articulated caudal vertebrae; right scapula and coracoid and portions of left scapula; right clavicle; interclavicle; left humerus; both ulnae; numerous carpal bones; one nearly complete articulated fore foot and numerous elements of the other; articulated pelvis with both hind limbs and feet complete. Collected by George F. Sternberg, July 22, 1937.
- U.S.N.M. No. 15569: Incomplete lower jaws without teeth, tibia, fibula, and a portion of a foot. Collected by George B. Pearce, July 23, 1937.
- U.S.N.M. No. 15573: Portion of a maxillary with teeth, fragmentary parts of both scapulae, parts of both humeri, astragalus, calcaneum, several foot bones, and numerous fragments. All parts weathered out. Collected by George F. Sternberg, July 22, 1937.

<sup>2</sup> Several additional specimens were collected by the 1940 Smithsonian Paleontological Expedition. To date skeletal parts of nearly 50 individuals have been found.

- U.S.N.M. No. 15816: Nearly complete articulated skeleton, lacking most of the tail, worked out in relief in the matrix. Collected by George F. Sternberg, 1938.
- U.S.N.M. No. 15817: Articulated hinder portion of the skeleton of a very large individual; 7 presacral, 2 sacral, and 22 caudal vertebrae in series; pelvis and both hind limbs and feet complete. Collected by George F. Sternberg, 1938.
- U.S.N.M. No. 15818: Fragmentary dentary; 8 presacral vertebrae; both humeri, left complete; both radii; an ulna; left scapula and coracoid; left clavicle; both ilia; both ischia; one pubis; numerous foot bones. Collected by George F. Sternberg, 1938.
- U.S.N.M. No. 15819: Series of 18 articulated vertebrae (2 sacrals, 9 caudals, 7 presacrals); incomplete ilium; right femur; tibia and a part of tarsus and foot; left fibula, tibia, tarsus, and part of left hind foot; numerous fragmentary vertebrae. Collected by Smithsonian Paleontological Expedition, 1938.

### THE SKELETON

In the pages to follow there is given a detailed description of practically the complete skeletal anatomy of *Polyglyphanodon*. Since the manuscript descriptive of the skull and skeleton and most of the pen and ink illustrations were prepared prior to the discovery of the very complete skeleton (U.S.N.M. No. 15816) shown in plate 25, it has been deemed expedient to retain the less perfect individual (U.S.N.M. No. 15477) as the type originally selected and to designate the other as the paratype. This somewhat unusual procedure was decided on, not only for the reasons mentioned above, but because of the desire to retain the better specimen in its articulated state in relief in the original matrix. This treatment of the specimen renders it unavailable for proper detailed illustration, or for complete description of the individual bones.

The paratype, as shown in plate 25, is lying prone on its belly, with the ribs distended and regularly spaced on each side of the line of vertebrae. The articulated limbs and feet are stretched out free of the body. The axial skeleton is practically complete from the tip of the skull to the eighth caudal vertebra. Only the twelfth vertebra from the skull and the tail beyond the eighth caudal vertebra are missing.

That the twelfth vertebra is lacking is indicated by a gap in the series and also by the presence of portions of both ribs that formerly articulated with it. All the elements of both the pectoral and pelvic girdles appear to be present, but some of these have been damaged by crushing and others cannot be exposed in their entirety because of the overlying spinal column.

The more important structural features of the skeleton displayed only by this specimen are: The complete presacral formula of 29 vertebrae; complete perforate clavicle; complete interclavicle; and complete digital formula of the manus. The skull is in more perfect preservation than the type and has furnished important supplemental information that has been incorporated not only in the descriptive matter but in the illustrations as well.



Views of the locality where the type and other specimens of *Polyglyphanodon sternbergi* Gilmore were found: *A*, Badland area of the North Horn formation (the man in the right center is standing at the spot where the type was collected); *B*, distant view of the lizard locality, the denuded area in the central part of the picture; Ferron Canyon is shown at the extreme right. Both photographs by C. L. Gazin.



## SKULL

The description of the skull is based primarily on the almost complete articulated cranium and lower jaws of the type specimen, U. S. N. M. No. 15477. It is supplemented by skull portions of three other specimens: U.S.N.M. No. 15816, the paratype; No. 15568, the greater portion of a disarticulated skull; and No. 15559, consisting of the articulated parietal and frontal and a left maxillary. The type has suffered some deformation through crushing, which has obscured structural details of the supratemporal and postorbital arches. Except for this, the right side of the skull is in good preservation, though the left side is slightly less well preserved.

Viewed laterally, the skull of *Polyglyphanodon* is subtriangular in outline, with heavy arches and a deep maxillary region. Except for the dentition the skull is normal lacertilian in all respects. The principal structural features of the skull are clearly illustrated in figures 16-19, drawn from the type, with some details added from the evidence furnished by other specimens.

*Parietal.*—The parietal (*p*) is relatively short, with flattened dorsal surface, and is transversely constricted posteriorly to its midlength. On each posterior external angle long, slender, divergent processes form much of the inner and posterior boundaries of the supratemporal fossae. Between these processes the posterior border is broadly hollowed out. Both of the posterior processes are missing in the type, but the right is preserved in its entirety in specimen U.S.N.M. No. 15568, and both are present in U.S.N.M. No. 15816. Anteriorly this bone joins the frontals by a straight, transverse digitating suture. This border at the center is deeply notched by the pineal foramen. Camp<sup>3</sup> observes: "The foramen is usually pierced between the parietals but, in the *Iguania* and *Rhoptoglossa*, where these bones are constricted posteriorly it sometimes migrates forward to lie in the frontoparietal suture."

The plane of the parietal is at a distinct angle to that of the frontal region, being depressed posteriorly. This angulation begins at the frontoparietal suture. On the anteroexternal angle the parietal articulates with the postfrontal, which sends a thin, widened process backward along the side of the parietal, as shown in figure 16. Along the anterior end the dorsal surface is roughened by a few ridges and grooves that extend slightly diagonal to the median axis. At the center the parietal of the type specimen measures 12 mm. in length, with a least transverse diameter of 9.4 mm.

<sup>3</sup> Camp, C. L., Classification of the lizards. Bull. Amer. Mus. Nat. Hist., vol. 48, p. 394, 1923.

*Frontal.*—The frontal (*f*) region of the type is checked and broken, so that much of the description is based on the better-preserved frontals of U.S.N.M. Nos. 15568 and 15816. In these specimens they are distinctly separate along the median line, but in the type specimen they are coossified. Their anterior ends unite with the nasals by a V-shaped suture that indents the ends of the frontals. Laterally the frontal articulates with the prefrontals and postfrontals much as in *Glyptosaurus*. The anterior and posterior processes of the postfrontals and prefrontals do not meet above the orbit but are separated by an interval of 6.5 mm. This space constitutes the frontal contribution to the boundary of the orbit. The lateral border above the

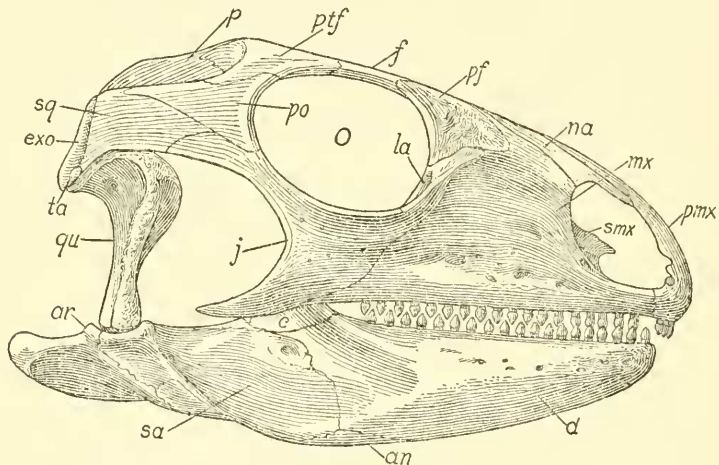


FIGURE 16.—Skull of *Polyglyphanodon sternbergi* Gilmore, U.S.N.M. No. 15477, type, natura size, viewed from the right side: *an*, Angular; *ar*, articular; *c*, coronoid; *d*, dentary; *exo*, exoccipital; *f*, frontal; *j*, jugal; *la*, lachrymal; *mx*, maxillary; *na*, nasal; *o*, orbit; *p*, parietal; *pf*, prefrontal; *pmx*, premaxillary; *po*, postorbital; *pf*, postfrontal; *sq*, squamosal; *ta*, tabulare; *sa*, surangular; *smx*, septomaxillary; *sq*, squamosal; *ta*, tabulare.

orbit is beveled from above downward and inward. On the ventral side, as shown by specimen U.S.N.M. No. 15559, the lower edge of the beveled surface forms a low-curved ridge that extends from one end of the bone to the other. The ridge becomes more prominent toward the anterior end, forming the lateral boundary of the olfactory portion of the brain. Between the orbits the frontals of the type specimen have a least transverse diameter of 10 mm. The dorsal surface is ornamented by a series of alternating transverse ridges and depressions.

*Nasals.*—The nasals (*na*) are irregularly shaped bones with long, slender anterior extremities that embrace the long posteriorly directed spine of the premaxillary, as shown in figure 17. Laterally the frontal articulates entirely with the maxilla, being excluded from contact with the prefrontal by the interposition of the slender,



superior process of the maxillary. The frontal contribution to the formation of the boundary of the external nares is damaged on both sides of the type skull, and this part of the restored skull has been drawn following U.S.N.M. No. 15816, which has this region completely preserved.

*Premaxillary.*—The premaxillary (*pmx*) has an unusually long spine that extends far posterior between the nasal bones. Viewed from above the nose is broadly rounded, the alveolar border giving support to six small premaxillary teeth. Laterally the premaxillary united with the maxillary by a straight vertical suture. Near the base of the spine, the border is scalloped by two small notches one above the other (see fig. 16).

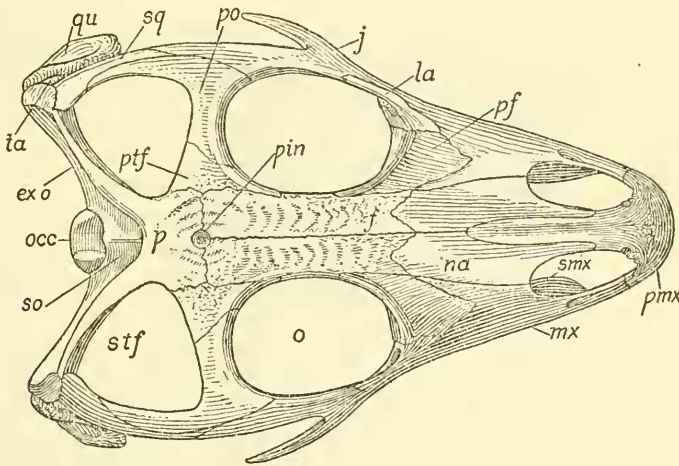


FIGURE 17.—Skull of *Polyglyphanodon sternbergi* Gilmore, U.S.N.M. No. 15477, type, natural size, viewed from the top: *exo*, Exoccipital; *f*, frontal; *j*, jugal; *la*, lachrymal; *mx*, maxillary; *na*, nasal; *o*, orbit; *occ*, occipital condyle; *p*, parietal; *pin*, pineal foramen; *pf*, prefrontal; *pmx*, premaxillary; *po*, postorbital; *ptf*, postfrontal; *qu*, quadrate; *smx*, septomaxillary; *so*, supraoccipital; *sq*, squamosal; *stf*, supratemporal fossa; *ta*, tabulare.

*Maxillary.*—The maxillary (*mx*) viewed from the side is subtriangular in outline and is unusually deep at the midline. The posterior end underlaps the jugal, its posterior end terminating below the center of the orbit. Above it articulates with the lachrymal, prefrontal, and nasal, interposing a slender pointed process posteriorly between the prefrontal and nasal bones, as in the agamid lizard *Hydrosaurus pustulosus*. This bone carries a full complement of 18 teeth, which occupy an alveolar space 32.6 mm. in length. The anterior end is deeply excavated to form the posterior and ventral boundaries of the anterior nares. The external surface of the bone is smooth except for a number of small foramina, three of which are arranged in a row slightly above, but nearly parallel to, the alveolar border.

*Septomaxillary.*—In the right nareal opening a small irregular shaped bone (*sma*, fig. 16), in contact with the inner side of the maxillary, is tentatively regarded as being the septomaxillary.

*Prefrontal.*—The prefrontal (*pf*) is a subtriangular bone whose posterior extremity along the side of the frontal terminates in front of the orbital center. Anteriorly, the bluntly pointed end is wedged in between the upper and lower posterior branches of the maxillary. The prefrontal does not have the usual contact with the nasal bone, being entirely separated from it by the interposition of the slender maxillary process. Ventrally it articulates with the lachrymal.

*Postfrontal.*—The postfrontal (*ptf*) is a triradiate element that articulates about equally with the parietal and frontal extending across their line of junction (see fig. 17). On the left side of the type skull, the postfrontal displays a squamous sutural border for union with the postorbital which looks downward and forward. On the right side, however, no trace of this sutural junction can be detected, a condition suggesting that in old individuals these two bones might become fully coalesced.

*Postorbital.*—That there was a distinct postorbital (*po*) bone in *Polyglyphanodon* is clearly indicated in the paratype, U.S.N.M. No. 15816, where the sutures delimiting this element are plain on both sides of the skull. It fills the interspace between the postfrontal and jugal, its anterior edge contributing much to the orbital border, as shown in figure 16. Posteriorly it unites by squamous suture with the squamosal, tapering out to a slender pointed process that lies upon the top border of the squamosal.

In some lizards the postorbital is fused with the postfrontal (*Ardeosaurus*), but according to Siebenrock it is entirely absent in *Crotaphytus* and most Agamidae.

*Lachrymal.*—The lachrymal (*la*), viewed laterally, is narrow and elongate dorsoventrally and in articulated position is wedged in between the jugal, maxillary, and prefrontal bones. Much of its outer surface forms a prominent diagonal ridge, which is a continuation of the upper jugal border. A large lachrymal foramen perforates the bone, the external opening of which is shown within the anterior rim of the orbit (see fig. 16).

*Jugal.*—The jugal (*j*) is deep and massive, with a long tapering spur that projects backward and downward from its posterior angle. This spurlike process is missing on the jugal of the type specimen, but the paratype has it completely preserved. Anteriorly this bone joins the lachrymal by a nearly horizontal suture, and it unites with the maxillary by a long, diagonal overlap. Posteriorly, its slender, upwardly directed process underlaps the postorbital and abuts the squamosal, as illustrated in figure 16. The jugal in *Polyglyphanodon*

is more massive, and the spurlike process is more extensively developed than in any lizard with which I have been able to make comparison.

*Squamosal*.—Both of the squamosal (*sq*) bones in the type skull are more or less damaged, but the paratype has both well preserved. They are relatively short bones, deep dorsoventrally, with a squarely truncate posterior end. This end is in contact with the paraoccipital process of the exoccipital, the posterior process of the parietal and the tabulare, and with them forms the posterior angle of the skull. It abuts the paraoccipital process of the exoccipital. On the lower side near the posterior end it is hollowed out by the cotylus for the articulation of the quadrate. Superiorly it joins the posterior branch

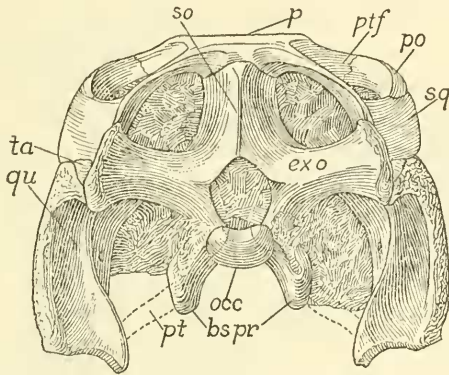


FIGURE 18.—Skull of *Polyglyphanodon sternbergi* Gilmore, U.S.N.M. No. 15477, type, natural size, posterior view: *bspr*, Basipterygoid processes; *exo*, exoccipitals; *occ*, occipital condyle; *p*, parietal; *po*, postorbital; *pt*, pterygoid; *ptf*, postfrontal; *qu*, quadrate; *so*, supraoccipital; *sq*, squamosal; *ta*, tabulare.

of the postorbital by squamous union, thus forming the supratemporal arcade. The full course of the squamosal-postorbital suture, as shown in figure 16, is derived largely from the evidence of the paratype.

*Tabulare*.—The presence of a tabulare (*ta*) is clearly indicated on the left side of the type specimen, where its posterior end is intercalated between the squamosal, quadrate, and paraoccipital process, as shown in figure 18.

*Quadrate*.—The right quadrate (*qu*) of the type is in beautiful preservation and in articulated position. Quadrates are also present in specimens U.S.N.M. Nos. 15559, 15556, and 15816. Viewed posteriorly the outer border, which is thickened and roughened, is bowed outward from end to end with a wide external conch. This border projects backward beyond the level of the adjacent surface. The articular proximal end is rounded anteroposteriorly and strongly overhangs the posterior surface. A sharp ridge develops at the base

of the head and continues downward in a diagonal direction to the inner side of the distal end. On the inner side a thin winglike process extends forward and inward from the main mass of the bone. The anterior face of the quadrate presents a shallowly concave front. The distal articular end is concave transversely and strongly convex anteroposteriorly, with a prominent downward projection of the inner border.

*Occiput.*—The occipital region of the type skull is practically complete, but two wide cracks passing horizontally through the back separate some of the bones, and this fact has necessitated some adjustments in drawing the reconstruction shown in figure 18. The sutures of the occipital region are all coalesced and can no longer be traced. The supraoccipital (*so*) is stout and has a sharp median ridge extending downward from the top to the foramen magnum. The exoccipitals (*exo*) form the lateral boundaries of the foramen. As shown by specimen U.S.N.M. No. 15568, where the exoccipitals are detached from the basioccipital, they participate in the formation of the occipital condyle (*occ*) (see fig. 18). The condyle is reniform and of relatively small size. The paraoccipital processes extend outward and backward, terminating in expanded ends that are in contact with the tabulare (*ta*), squamosal (*sq*), and quadrate (*qu*).

*Palate.*—The palate of the type skull, U.S.N.M. No. 15477, although distorted by the lateral crushing of the cranium, displays most of its important features. It has been skillfully reconstructed by Mr. Prentice in figure 19 and, while errors of detail may eventually be shown, it is believed the more important structures are correctly interpreted.

The basioccipital and basisphenoid are fully coossified, no trace remaining of their sutural junction. The basioccipital processes (*bspr*) are stout rounded projections that extend downward and slightly outward, with rounded obtuse distal terminations. The basisphenoid (*bsp*) at its anterior external angles develops a pair of strong divergent processes, the dilated extremities of which articulate with longitudinally elongated facets on the medial sides of the pterygoids. The pterygoids (*pt*), widely divergent posteriorly, are in contact with the quadrates. On their inner sides, slightly posterior to their midlength, they are in articulation with the basisphenoid processes. The slender, posterior, barlike portions of the pterygoids have their greatest diameters nearly vertical, and it is assumed they were longitudinally hollowed out, as in *Iguana*. Forward of the contact with the basisphenoid processes the pterygoids widen transversely, their widened anterior ends articulating with the palatines (*pal*). There are no teeth on the pterygoid bones, but at about midlength the palatal surfaces are traversed transversely by a low, sharp ridge that extends across nearly the whole width of the bone. Opposite the ridge the

pterygoids develop robust downwardly projecting processes that articulate by squamous sutures on the external sides with the strongly developed ectopterygoid (*ecpt*) bones, which are interposed between them and the maxillaries (*mæ*) as shown in figure 19.

The sutural contact of pterygoids and palatines is by a diagonal suture that starts at about midlength of the pterygomaxillary vacuity (*ptmæv*) and extends inward and forward toward the median line. The palatines appear to be narrowly separate on the midline, at least posteriorly; anteriorly they may have been in apposition, as in *Iguana*. Anteriorly the palatines are relatively slender and join the vomers by a long diagonal overlapping suture. Posterior to midlength the right palatine develops a thin outwardly directed process that laps along the

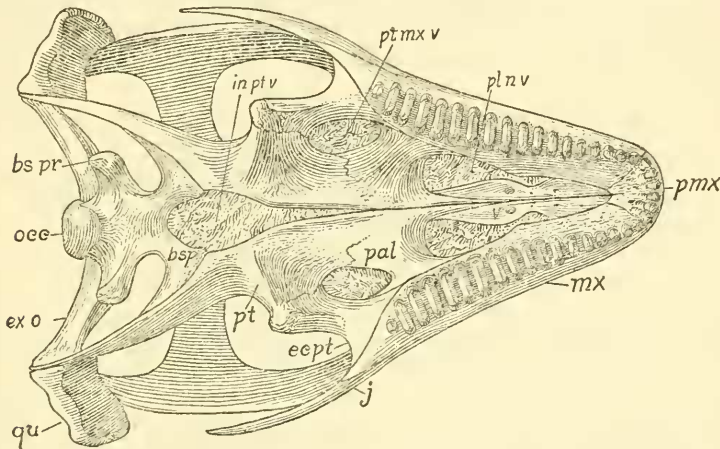


FIGURE 19.—Palate of *Polyglyphanodon sternbergi* Gilmore, U.S.N.M. No. 15477, type, natural size: *bsp*, Basisphenoid; *bspr*, basioccipital process; *ecpt*, ectopterygoid; *exo*, exoccipital; *inptv*, interpterygoid vacuity; *j*, jugal; *mx*, maxillary; *occ*, occipital condyle; *pal*, palatine; *plnv*, palatonarial vacuity; *pmx*, premaxillary; *pt*, pterygoid; *ptmæv*, pterygomaxillary vacuity; *qu*, quadrate; *v*, vomere.

inner side of the maxillary. This process forms the posterior boundary of the palatonarial vacuity.

The vomers (*v*) are distinct but closely applied to one another along the median line. Their forward ends are received in a concave notch on the posterior sides of the premaxillaries. Laterally, forward of the constriction, they also appear to be in contact with the maxillaries, as shown in figure 19. There are five important vacuities in the bony palate. The interpterygoid vacuity (*inptv*) is a single median aperture, bounded laterally by the pterygoids, and probably extending some way between the palatines; posteriorly it is bounded by the hypophyses of the basisphenoid. The pterygomaxillary vacuity in *Polyglyphanodon*, as contrasted with those of *Iguana*, are much reduced in size.

They are bounded outwardly by the maxillary and ectopterygoid, inwardly by the pterygoid and palatine, in front by the palatine, and behind by the pterygoid and ectopterygoid.

The palatonares, also paired vacuities, are long and narrow, bounded externally by the maxillary, internally by the vomer and palatine, posteriorly by the palatine.

In addition to these usual openings, the vomer is perforated near its anterior end by a small foramen, and there appears to be an aperture through the palatine near its posterior end.

The palate of *Polyglyphanodon* in its general design resembles that of the *Iguana*, especially in the robustness of the downwardly projecting pterygoid process, and the stout ectopterygoid and the manner of its attachment to the posterior end of the maxillary. It differs in the much reduced size of the pterygomaxillary vacuities, and the more posterior position of the palatine processes that unite with the maxillary.

*Measurements.*—Comparative skull measurements (in millimeters) are as follows:

	Type	Paratype
Greatest length over all.....	81.5	80.0
Greatest width across tops of quadrates.....	45.0 <sup>e</sup>	52.0
Greatest width across jugals.....	-----	58.5
Greatest width across center of nares.....	14.0	14.0
Least width of parietal at center.....	9.5	8.5
Least width of frontal at center.....	11.0	12.0
Greatest height of skull with lower jaws.....	60.8	----
Diameter of orbit anteroposteriorly.....	-----	27.0
Vertical diameter of orbit.....	25 <sup>e</sup>	21.0
Greatest length of quadrate.....	31	----
Greatest length of squamosal.....	-----	16.0
Greatest length of frontal.....	35 <sup>e</sup>	32.2
Greatest length of parietal.....	-----	19.0
Greatest width of occipital condyle.....	9	----

e=estimated

#### LOWER JAW

The rami of the type specimen are in excellent preservation and in articulated position with the skull, but many of the sutures are indistinct. In all there were seven other rami in the collection, and from a study of all it has been possible to delimit most of the individual elements of the mandible and to determine it as consisting of six distinct bones: dentary, angular, surangular, articular, coronoid, and splenial. It is assumed that the prearticular is present but fused with the articular, as it is in most adult lizards.

The ramus as a whole is strong and massive, deepest at the center and narrowing toward the ends.

*Dentary.*—The dentary gives support to 19 teeth, and viewed from above, as in figure 21, it has a sinuous dental border, the anterior end curving inward to meet its fellow of the opposite side. On the inner side of the anterior end a rounded, flattened surface indicates the extent of their union at the symphysis (see fig. 20). The dentary-surangular suture lies below the anterior half of the coronoid, much as in *Peltosaurus*.

*Angular.*—The angular (*an*) in a lateral view is slightly visible on the mid lower border and again where its posterior extremity turns upward toward the articular. In its limited participation in the lateral surface of the ramus, the angular has its closest approximation in the Agamidae. On the inner side it probably underlies the prearticular and at the forward end is in contact with the splenial and dentary. On the inner side near the upper anterior end the angular

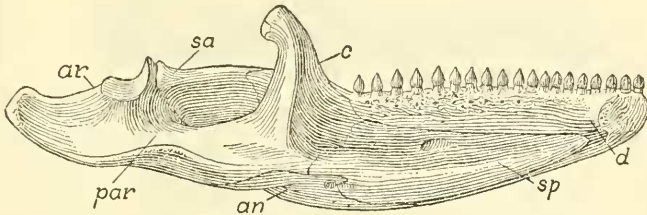


FIGURE 20.—Left ramus of *Polyglyphanodon sternbergi* Gilmore, U.S.N.M. No. 15477, type, internal view, natural size: *an*, Angular; *ar*, articular; *c*, coronoid; *d*, dentary; *par*, prearticular; *sa*, surangular; *sp*, splenial.

is perforated by a small foremen (see fig. 20). Its long tapering anterior extremity is intercalated between the splenial and dentary.

*Surangular.*—The surangular (*sa*) is relatively short and deep and comprises practically all the area between the dentary and the articular on the external side of the ramus, as clearly shown in figure 16. Near its posterior end a prominent sharp ridge extends from the anterior border of the cotylus diagonally downward and forward across the whole depth of the bone, much as in *Cyclura*. On the inner side a nearly vertical suture shows its union posteriorly with the articular (see fig. 20). Anteriorly it unites with the coronoid. Its sutural articulation with the prearticular is so fully coalesced that it cannot be traced in any of the materials now available.

*Coronoid.*—The coronoid (*c*) rises prominently above the general level of the ramus, with a decided backward bend near its upper extremity. On its inner side a sharp median perpendicular ridge extends from almost the top to the bottom of this bone, thus giving it additional strength. The ventral border on the internal side probably meets the anterior end of the prearticular, but the sutures in all

available specimens have been obliterated. Anteriorly it meets the dentary and splenial.

*Articular.*—The articular (*ar*) forms the entire angle of the jaw. The end posterior to the cotylus is gently incurved and has a bluntly truncated termination. Viewed externally the whole surface from the top downward strongly recedes inward. The upper border immediately posterior to the cotylus is deeply concave. The cotylus is shallowly concave anteroposteriorly, bifossate. It has a greatest width of 7.5 mm. Most of its outer wall is formed by the surangular.

*Splenial.*—The splenial (*sp*) is a thin triangular shaped bone that laps along the lower inner side of the dentary. Its pointed anterior extremity ends short of the symphysis. Except at the anterior end it completely covers Meckel's groove and in a lateral view is not

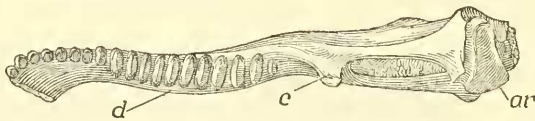


FIGURE 21.—Right ramus of *Polyglyphanodon sternbergi* Gilmore, U.S.N.M. No. 15568, superior view, natural size: *ar*, Articular; *c*, coronoid; *d*, dentary.

visible on the lower border. A foramen perforates its upper median border. The large size and great anteroposterior extent of the splenial in *Polyglyphanodon* shows a striking distinction from the small, limited splenial of *Cyclura* and *Iguana* or the very small splenial found in the Agamidae.

*Precarticular.*—Although the precarticular is indicated in figure 20, I have been unable to delimit its boundaries.

*Measurements.*—The measurements of the ramus of the type, U.S.N.M. No. 15477, are as follows (in millimeters):

Greatest length.....	85.5
Greatest depth at posterior end of tooth row.....	16.5
Depth of ramus at anterior end.....	5.5
Depth of ramus to top of coronoid.....	24.3
Transverse width at middle of tooth series.....	5.7

*Differences.*—The splenial is very small or absent in the Agamidae, and the dentary has the greatest posterior extent in the Chamaeleonidae and Agamidae, either being a feature that would disbar *Polyglyphanodon*. The Meckelian groove is open in Chamaeleonidae, Agamidae, and Varanidae but is roofed over more or less completely in all other families, as it is in *Polyglyphanodon*.

#### TEETH

The outstanding feature of *Polyglyphanodon sternbergi* is the transverse widening of the teeth of the posterior half of the dental



series, a style of dentition never before observed in the Sauria, either living or extinct (see figs. 19 and 21). These teeth display a sharp transverse cutting edge, with a subtriangular cusp on the outer edge in both upper and lower teeth. There is no indication of median

cusps, as in the teeth of *Diadectes* or *Trilophosaurus*, to which these teeth have a resemblance in their great transverse width. This smooth, sharp-edged crown is smoothly beveled on both sides of the cutting edge. The sides of the teeth swell out and then contract sharply to the root. The lower teeth fit between the upper teeth when the jaws are closed, thus closely interlocking.

The anterior teeth in external view are conical, but on the inner side the crowns are slightly excavated dorsoventrally on each side of an incipient median ridge (see C and D, fig. 22). This vertical ridge grows progressively more prominent in a posterior direction. On the eighth lower tooth (fig. 21) and seventh upper tooth, it suddenly extends laterally into a sharp cutting edge on the crown, the whole crown being about one-half the width of the next tooth posteriorly. The succeeding teeth grow progressively wider, reaching the maximum size on the tenth. Those following remain constant in diameter as far as the seventeenth, which is perceptibly narrowed. The last or eighteenth tooth in the maxillary and the last or nineteenth tooth in the dentary are greatly reduced and conical, with faint inner vertical ridge.

The complete dentition of *Polyglyphanodon* as indicated by the type specimen shows the dental formula to be as follows:

$$\frac{\text{maxillary } 18, \text{ premaxillary } 3}{\text{dentary } 19} = \frac{42}{38}$$

The teeth are heterodont and ankylosed to the jaw bones in shallow pits that are regarded as subacrodont in character of implantation. These shallow depressions for the teeth in no way correspond to the alveoli of the typical thecodont attachment but are more like those of the Amphibia. There is no uniformity of opinion as to what kind of tooth insertion is oldest in the Sauria. The fossil record seems to indicate that thecodonty has preceded both pleurodonty and acrodonty, as pointed out by Camp.<sup>4</sup> The teeth are solid, and in none of the specimens is there evidence of replacement teeth.

<sup>4</sup> Camp, C. L., Classification of the lizards. Bull. Amer. Mus. Nat. Hist., vol. 48, p. 364, 1923.

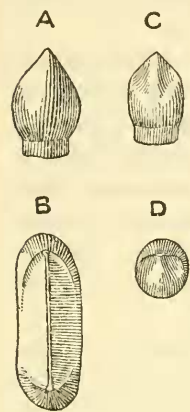


FIGURE 22.—Lower teeth of *Polyglyphanodon sternbergi* Gilmore, U.S. N.M. No. 15568, all five times natural size: A, Fourteenth tooth, enumerated from the front, lateral view; B, same, top view; C, fourth tooth, internal view; D, same, top view.

## VERTEBRAE

The vertebral column is represented by relatively long articulated series in 4 of the 12 known individuals, besides a considerable number of short series and separate vertebrae belonging to other specimens. From a study of all, most of the column is known except the distal half of the tail.

All the vertebrae are procoelous. The vertebral column is best represented in specimen U.S.N.M. No. 15816 (see pl. 25), which has 39 articulated vertebrae present. Twenty-nine of these are presacral, two sacral, and eight anterior caudals. Beginning with the atlas, 11 are articulated in series. A short gap separates the eleventh and thirteenth, but posterior to this interval they form a continuous series ending with the eighth caudal. That the twelfth vertebra is missing is indicated by the presence in sequential position of parts of both ribs that formerly articulated with it, as shown in plate 25.

In view of the little disturbed condition of the vertebrae with practically all the ribs in articulated position, it would appear that 29 represents the complete presacral series. A skeleton of *Iguana*, in comparison, has 24 presacral vertebrae.

How many of these are to be designated cervical depends entirely on how the count is made. Most authorities regard all vertebrae whose ribs attain a connection with the sternum as belonging to the dorsal series. This criterion, however, is of little practical use with fossil specimens, since the evidence of such a connection is seldom preserved. In the present specimen the spinous processes undergo a distinct change on the ninth vertebra, and this may indicate the point of division between cervical and dorsal. If so, there would be 8 cervicals and 21 dorsals, but the presence of long ribs articulated with the seventh and eighth vertebrae in specimens U.S.N.M. Nos. 15816 and 15566 appears to indicate adequately that these vertebrae were attached to the sternum as in *Iguana* and are therefore dorsal. There are no lumbar, for the last presacral bears a short rib, as shown by three specimens.

The sacrum is composed of two noncoalesced vertebrae, as shown by the type and by U.S.N.M. Nos. 15566 and 15816.

The total number of caudal vertebrae cannot be determined from available specimens. Specimen U.S.N.M. No. 15817 (see plate 25) has a series of 19 vertebrae of the anterior portion of the tail, articulated in series with the sacrals, and when these are compared with those of an *Iguana* of the same size they appear to indicate a tail of about equal length and proportions. The restoration in plate 26 has been given 48 vertebrae in the tail, with a total length of about 18 inches.

The vertebral formula of *Polyglyphanodon sternbergi*, as known at this time, may be stated as C-6; D-23; S-2: CD (48±).

*Atlas*.—The atlas is present only in specimen U.S.N.M. No. 15816, and as it remains in the original articulated position it is not available for detailed study. The neurapophyses are seen to arch over the neural canal, though separate on the median line, and a backward-projecting process carries the posterior zygapophysis for articulation with the axis. All other parts of this bone remain hidden in the matrix.

*Axis*.—The detailed description of the axis is to a great extent based on that of the type, only the incomplete spine being restored after the axis of U.S.N.M. No. 15816, as shown in figure 23. This element is also present in specimens U.S.N.M. Nos. 15566 and 15568, but both are less well preserved.

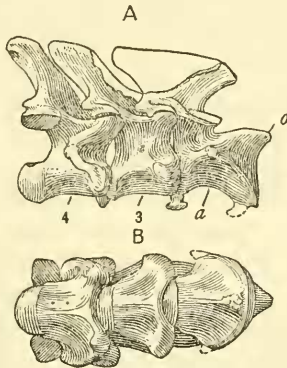


FIGURE 23.—Cervical vertebrae of *Polyglyphanodon sternbergi* Gilmore, U.S.N.M. No. 15477, type, natural size: A, Lateral view; B, ventral view. *a*, Axis; *o*, odontoid; 3 and 4, third and fourth cervicals, respectively.

In the type the axis was found articulated with the third and fourth cervicals, and a detached vertebra appears to represent the fifth. The anterior end of the centrum of the axis is broadly expanded, with the odontoid of the atlas completely fused with it. The articular surface of this end is broadly rounded from side to side and is much deeper dorsoventrally than the axis of an *Iguana* of corresponding size. This face in the type has a greatest width of 11.25 mm. and a greatest depth of 8.75 mm., and the length of the centrum is 13.5 mm. Viewed from below, in front of the ball the centrum is regularly rounded from side to side, but the forward half is pinched together to form a sharp-edged process that projects downward on the median line (see B, fig. 23). This process may represent the fused axis intercentrum, although no trace of the line of coalescence is now discernible in any of the specimens. A small, rounded, spurlike, backward-directed diapophysial process is present on each side of the upper anterior end of the centrum. Prezygapophyses and postzygapophyses are well developed. The spinous process is incomplete in the type and has been restored in figure 23 from U.S.N.M. No. 15816. It resembles the neural spine of *Iguana*.

As in that genus, it strongly overhangs the anterior half of the centrum and presents a thickened anterior border that is slightly hollowed out longitudinally.

*Cervical vertebrae posterior to the axis.*—Six vertebrae are considered as constituting the complete cervical series. The type specimen has the second, third, fourth, and fifth cervicals preserved, whereas all are present in U.S.N.M. No. 15816. The principal modification to be observed between the third and sixth vertebrae, inclusive, is an increase in size of the diapophyses and a progressively more erect posture of the neural spines. The neural spines are relatively narrow anteroposteriorly, with a thickened posterior border and a sharp anterior edge. The top is thickened transversely, with a diagonally truncated end that in the posterior members of the cervical region is broadly notched. The sixth spine is perceptibly widened fore and aft. A small diapophysial process on the third cervical may have borne a small cervical rib, as indicated by the smooth articular surface of its end. This process on the fourth cervical is more robust, being elongated dorsoventrally and constricted near the middle, thus dividing the articular surface into two costal facets. These facets have a decided diagonal trend, the lower border projecting downward slightly below the level of the centrum on the fifth and presumably on the sixth cervical. The diapophyses reach their maximum size on the sixth. The centra are relatively short, subequal in size, evenly rounded on the ventral surface, and have a subcircular ball and cup. A heavy rounded ridge runs diagonally downward and backward from the top of the diapophyses to the edge of the ball. Below this ridge the side of the centrum is slightly excavated. The ridge joining the prezygapophyses and postzygapophyses is broadly hollowed out at the center. All these vertebrae have a well-developed zygantral-zygantrum articulation.

Intercentra are present in articulated position in specimen U.S.N.M. No. 15566, at the junction of the second and third and of the third and fourth cervicals, as clearly shown in plate 25. There are no distinct articulating facets for these elements, as in *Iguana* and *Cyclura*, their broadened bases resting smoothly across the junction of the centra. As mentioned previously, the downward-projecting process on the anterior ventral border of the axis may be a coalesced intercentrum.

As articulated, the five anterior vertebrae in specimen U.S.N.M. No. 15566 have a total length of about 64 mm.

Measurements of cervical vertebrae of the type (U.S.N.M. 15477) (in millimeters)

	2	3	4	5
Greatest length of centrum-----	10.5	10	10	10.75
Greatest transverse width across diapophyses-----	13	13.0	13.6	15.5
Greatest height over all-----	16	21.75	21.9	21.9

*Dorsal vertebrae.*—Including the one that is missing, the presacral series in specimen U.S.N.M. No. 15816 (pl. 25) consists of 23 vertebrae. The detailed description to follow is based, however, to a great extent on the vertebrae of specimen U.S.N.M. No. 15566, since they have been more completely freed from the matrix than those of the paratype. Seen from below, the centra are tapering in outline, depressed, with subovate condyle and a glenoid fossa. Nowhere is there evidence of a ventral keel or carina, the ventral surface being broadly rounded from side to side in the anterior part of the dorsal series and flattened in the posterior part. The series is greatly similar in structure throughout. The first and second dorsals have narrowed spines, but beginning on the third the neural spines are wide anteroposteriorly, with a nearly vertical posterior border and a long sloping anterior border. This style of spine, of uniform height, prevails to the twentieth vertebra. On the three posterior dorsals the anteroposterior diameter of the top portion of the spines suddenly contracts, and the tops are squarely truncate, with a very slight transverse expansion of this end.

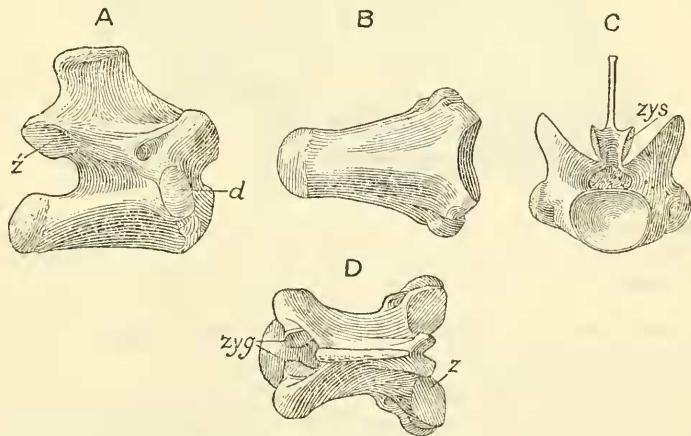


FIGURE 24.—Median dorsal vertebra of *Polyglyphanodon sternbergi* Gilmore, U.S.N.M. No. 15566, natural size: A, Lateral view; B, ventral view; C, anterior view; D, dorsal view. *d*, Diapophysis; *z*, anterior zygapophysis; *z'*, posterior zygapophysis; *zyg*, zygosphenes; *zys*, zygosphenes.

The centra to the middle of the thoracic series gradually lengthen and then posteriorly continue with little change in length as far as the twenty-second dorsal. The twenty-third has the centrum decidedly shortened, as shown by the type specimen, which has the twenty-second, twenty-third, and sacrum articulated (see fig. 26). For example, measured along the center of the ventral side from the edge of the cup to the beginning of the ball the twenty-second is 14 mm., whereas the twenty-third or last dorsal is only 11 mm. in length.

Viewed from the side a prominent rounded ridge extends from the base of the diapophyses diagonally downward and backward, merging

into the centrum at the constriction for the ball. Below this ridge the side of the centrum is slightly hollowed out, this feature being most prominently developed in the anterior half of the series and tending to fade out in the direction of the sacrum. Above this ridge and between it and the less conspicuous ridge joining the prezygapophyses and postzygapophyses there is a slight excavation of the surface that widens posteriorly.

Anteriorly the diapophyses stand out prominently from the sides of the centra and are about equally supported by the centra and neuropophyses. The costal facets for the ribs on the anterior dorsals are subovate, with the longer diameter nearly vertical (see fig. 24). These facets gradually increase in size on the first five dorsals, remain subequal on the next three, and, beginning with the ninth or tenth, are progressively reduced in size and changed in outline from oval to semicircular (see fig. 25). A small zygosphene-zygantrum articulation is developed on all the dorsals (fig. 24). These are more fully functional than the rudimentary stage found in the varanid lizard *Saniwa*.

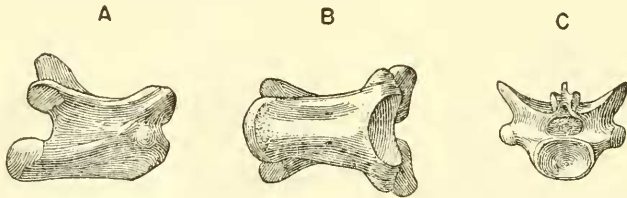


FIGURE 25.—Posterior dorsal vertebra of *Polyglyptanodon sternbergi* Gilmore, U.S.N.M. No. 15477, type, natural size: A, Lateral view; B, ventral view; C, anterior view; spine largely missing.

Measured along the top the 23 dorsal vertebrae in specimen U.S.N.M. No. 15816 have a total length of about 350 mm.

*Sacral vertebrae.*—The sacrum consists of two vertebrae, and in none of the specimens is there indication of coalescence. The anterior sacral is slightly stouter than the posterior one and bears the heaviest sacral rib. These ribs are attached to the anterior two-thirds of the sides of the centra, their ventral surfaces being only slightly above the ventral level of the centra (see fig. 26). The ribs in all available specimens are completely coalesced, with no trace of their sutural union with the centrum.

Seen from below, the sacral centra are broadly rounded transversely and provided with the usual cup and ball. The spines are narrowed anteroposteriorly as contrasted with the wide spinous processes of the dorsals. Both vertebrae are provided with zygosphene-zygantrum articulation in addition to the regular zygapophyses.

The sacral ribs are long, the rib of the first sacral projecting straight outward from the centrum, the rib of the second outward and forward, as shown in figure 26. The ventral surface of the second is indented

near its proximal end by a longitudinal groove that extends outward for a third of its length. The second ribs are slenderer than the first, and their outer ends are expanded, with the anterior edges abutting the posterior border of the first ribs and thus enclosing ovate sacral foramina. Viewed laterally, the ends of the ribs form the periphery of a half circle, thus forming a deep cavity between them that is open on the dorsal side.

*Measurement of the sacrals of the type (U.S.N.M. No. 15477) (in millimeters)*

Greatest length of the two centra.....	33
Greatest width from tip to tip of the first sacral rib.....	62
Greatest height over all of sacral two.....	23

*Caudal vertebrae.*—The tail of *Polyglyphanodon* is represented by two articulated series of caudals and a few scattered vertebrae. Specimen U.S.N.M. No. 15817, which has the best-preserved section of the

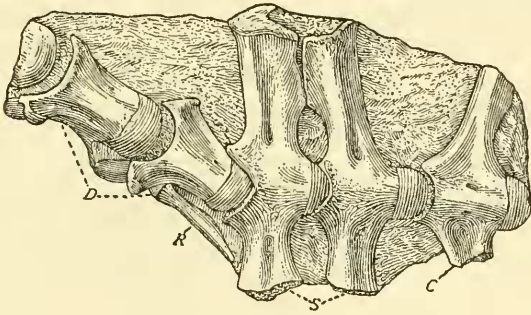


FIGURE 26.—Dorsal, sacral, and caudal vertebrae of *Polyglyphanodon sternbergi* Gilmore, U.S.N.M. No. 15477, type, ventral view, natural size: C, First caudal vertebra; D, dorsal vertebrae; R, last thoracic rib; S, sacral vertebrae.

tail, consists of  $18\frac{1}{2}$  vertebrae that are in articulation with the sacrum, with parts of four others slightly separated from the last one of the series, as shown in plate 25. Specimen U.S.N.M. No. 15568 has an anterior caudal series of 22 vertebrae. A study of these two series seems to show that six anterior caudals are missing from U.S.N.M. No. 15568, so that we have knowledge of the first 28 vertebrae of the tail. The distal portion is missing in all specimens now available. In the restoration, plate 26, the missing portion of the tail has been restored after the *Iguana*, which *Polyglyphanodon* appears to resemble in many respects.

The first caudal vertebra has a centrum that is subequal in length with the last sacral and retains the depressed cup and ball of the pre-sacral region. The centra, beginning with the second, gradually increase in length posteriorly, but whether this lengthening continues into the distal portion of the tail cannot be determined from available materials. The first caudal has long, flattened transverse processes that extend outward horizontally from the sides of the centrum

with a decided backward inclination. On the succeeding caudals these processes grow progressively shorter until on caudal 15 only a faint spur remains. With the disappearance of the transverse processes the sides of the vertebrae are flattened, resembling those of *Iguana* in that respect. Zygapophyses are short and stout, and a well-developed zygosphene and zyganttrum are present in the anterior caudals, but how far they continue posteriorly cannot be determined. The spinous processes regularly increase in height to the neighborhood of the tenth caudal, reaching their maximum development there. From this point posteriorly they grow progressively shorter and become more slender. They also change in inclination in the first ten caudals from a type in which each strongly overhangs the succeeding vertebra to the nearly erect type of the tenth, which type then continues posteriorly.

On the ventral surface close to the beginning of the ball a pair of short articular protuberances indicates the points of attachment for the chevron.

#### CHEVRONS

The chevron bones of the anterior caudal region are long, slender, and subequal in length with the spinous processes. They articulate intervertebrately, but more especially with the anterior vertebra of each pair. The first chevron appears to be articulated with the third and fourth caudal instead of the second and third, as in *Iguana*.

#### RIBS

All the presacral vertebrae with the exception of the atlas, and possibly the axis, appear to have been rib bearing. The fifth cervical vertebra of the type specimen has the rib of the left side preserved in articulated position. It is short, having a head widely expanded dorsoventrally, with a cupped articular end that fully covers the elongated costal facet of the vertebra. The downwardly curved shaft tapers rapidly to a pointed distal end. Beginning well toward the proximal end on the median anterior surface an overhanging ridge projects prominently forward from this side. This ridge has a diagonal downward trend and merges into the outer ventral margin of the bone. Two cervical ribs belong to specimen U.S.N.M. No. 15568, one of which, as indicated by its smaller size, pertains to a cervical in advance of the fifth. It has a greatest length of 15 mm. On the left side of specimen U.S.N.M. No. 15816 cervical ribs 4 and 5 are preserved nearly in articulated position.

The thoracic ribs are best preserved in specimen U.S.N.M. No. 15816, as shown in plate 25. In all, 43 ribs are present, of which 30 are complete or nearly so, and practically all have been preserved articulated with their respective vertebrae. In specimen U.S.N.M. No. 15568 18 ribs are preserved; 9 of these on the left side are articu-



lated with the vertebrae, while 6 posterior ribs of the right side were found in such relationship as to be directly attributable to their proper places in the series.

The most anterior rib to be considered thoracic is articulated with the seventh vertebra in both specimens. It is thought to be the first rib to be connected with the sternum. It is on the basis of this evidence that the anterior six vertebrae are regarded as constituting the complete cervical series.

All the ribs are slender, single-headed, and curved gently nearly in one plane. On the anterior face of the proximal third of the anterior ribs is a longitudinal ridge that becomes progressively less and less pronounced but nowhere does this ridge overhang as in the cervicals. The posterior face for one-fourth of the length near the proximal end is traversed by a longitudinal groove. The ribs increase in length from the first to the thirteenth, and posterior to the thirteenth they shorten progressively. The length (in millimeters) of the complete ribs of specimen U.S.N.M. No. 15816 are as follows: First, 36; second, 41.6; third, 45; fifth, 55; eighth, 69; ninth, 71; tenth, 71; eleventh, 71, twelfth, 72.5; thirteenth, 74; fourteenth, 72.9; fifteenth, 62.4; twenty-third, 14.5.

The posterior ribs have nearly straight shafts, and there is a gradual reduction in size of the head from front to back. This reduction in the size of the head is in conformity with the diminution in size of the costal facets of the vertebrae. In the type the twenty-third or last rib is completely preserved *in situ* and has a greatest length of 12.5 m.

Thoracic ribs 9 and 10 of specimen U.S.N.M. No. 15816 show an exostosis of the bone on their upper thirds, suggesting that they had suffered injury and had healed in life. At the ends of several of the median ribs are ossifications that suggest strongly the presence of ossified sternal ribs. These may be plainly seen in plate 25.

#### PECTORAL GIRDLE

The ossified pectoral girdle is composed of the scapula, coracoid, clavicle, and interclavicle. Parts of the girdle are present in all the better-preserved specimens.

*Scapula-coracoid.*—The right scapula-coracoid of specimen U.S.N.M. No. 15559 is nearly complete, as shown in figure 27, and the detailed description to follow is based on this bone. The scapula is relatively broad and heavy for its length. The upper end is expanded, with a truncated end that is slightly convex anteroposteriorly. The missing portion of the end has been restored after specimen U.S.N.M. No. 15818. A small portion of the ossified suprascapula remains attached to this end, as shown in figure 27, *ssc*. The sinuous posterior border is thickened and rounded throughout the greater part of its length;

the anterior margin thin and emarginated. There is only one emargination, but since the proscapular process is missing, its full extent cannot be positively determined.

On the external surface a strong rounded ridge is developed immediately above the glenoid border and extends diagonally upward to the middle of the upper end, terminating in a raised end short of the upper border. The glenoid end is much thickened, having a greatest transverse width of 8 mm. In this specimen the coracoscapular articulation is so fully fused that all trace of their union has been obliterated. In the scapula-coracoid of U.S.N.M. No. 15568, however, this suture is indicated as continuing nearly straight through from the glenoid fossa to the anterior edge of the scapula above the procoracoid process, ending at the base of the scapula-coracoid fenestra.

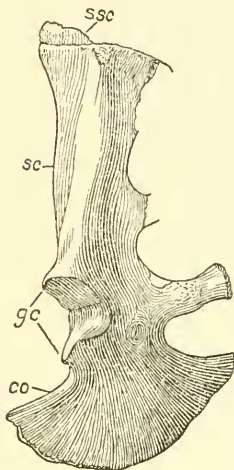


FIGURE 27.—Right scapula-coracoid of *Polyglyptanodon sternbergi* Gilmore, U.S.N.M. No. 15559, natural size, lateral view: *co*, Coracoid; *gc*, glenoid fossa; *sc*, scapula; *ssc*, fragment of the proscapula.

The coracoid is complete in U.S.N.M. No. 15559, as shown in figure 27. The coracoid has a single fenestra, as contrasted with two in most members of the Iguanidae. Between the posterior border of this fenestra and the glenoid fossa the bone is perforated by a large coracoid foramen. The proglenoid process is thickened and rounded. The ventral border forms a long, sweeping, convex curve. The coalesced coracoid and scapula have a greatest length over all of 68 mm.; the upper end of the scapula has a greatest anteroposterior diameter of 14.5 mm.; greatest anterior posterior diameter of the coracoid is 31 mm.

The presence of a single emargination in the coracoid suggests relationship with the Agamidae, which generally have but one, *Uromastrix* being an exception. However, little dependence as to relationship can be placed on this feature, for, as pointed out above, most Iguanidae have double coracoidal emarginations. Yet here again there are exceptions, for in the terrestrial genera *Urocentrum*, *Sceloporus*, and *Phrynosoma*, and in the Anolidae, there is but one. Usually these emarginations are enclosed anteriorly by the cartilaginous coracoidal and scapular borders; sometimes they are simply open emarginations.

*Clavicle*.—Clavicle bones are present in five individuals of the present collection, but only two, U.S.N.M. Nos. 15816 and 15818, have the expanded perforate, lower ends preserved. The description to follow is based on the left clavicle of the paratype, U.S.N.M. No. 15816, which is preserved in nearly its normal articulated position.

The clavicle of *Polyglyphanodon* is a simple curved bar, perforated near its expanded lower end by a subovate fenestra. The upper portion is narrow, but the shaft gradually widens in a ventral direction. Approaching the fenestra the posterior border abruptly widens and then maintains its width to the truncated interclavicular end, as shown in figure 28.

The concave margin of this bone is slightly thickened and rounded, but the opposite side is thin, presenting a sharp edge for much of its length. The posterior side of the distal half is hollowed out longitudinally. Its greatest length measured in a straight line from end to end is 50.8 mm.

On the whole this bone bears a strikingly close resemblance to the clavicle of the iguanid lizard *Lacmancetus*, the chief difference being in the more dorsal placement of the fenestra in the clavicle of the extant form.

Camp<sup>5</sup> was of the opinion that broadly expanded, nonperforate clavicles are ancestral among modern Sauria and that simple rounded clavicles have been shaped from these. The perforate clavicle of the present specimen shows that this type originated very much earlier than was previously known and to that extent does not give support to Camp's conclusion.

*Interclavicle.*—The interclavicle of *Polyglyphanodon sternbergi* may be described as cruciform, with a bifurcated anterior extremity and a long flattened posterior bar, the posterior end being obtusely pointed. This element is present in four specimens, U.S.N.M. Nos. 15559, 15566, 15568, and 15816,

all being slightly imperfect. The complete cross bar is preserved only in U.S.N.M. No. 15816, but in this specimen it is slender, with a slight curve posteriorly. Forward of this bar the shaft is constricted, but still farther forward it rapidly widens into two flattened divergent processes that are separated on the anterior end by a wide shall-

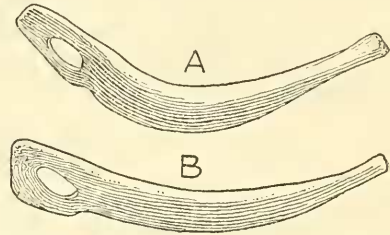


FIGURE 28.—Left clavicle of *Polyglyphanodon sternbergi* Gilmore, U.S.N.M. No. 15816, natural size: A, Oblique view drawn as it lay in the matrix; B, a direct side view.

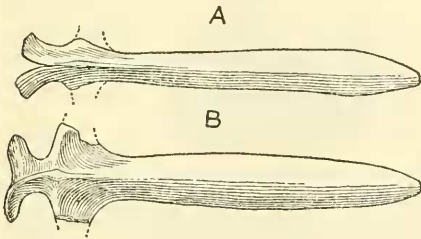


FIGURE 29.—Interclavicles of *Polyglyphanodon sternbergi* Gilmore, ventral views, natural size: A, U.S.N.M. No. 15559; B, U.S.N.M. No. 15568.

<sup>5</sup> Camp, C. L., Classification of the lizards. Bull. Amer. Mus. Nat. Hist., vol. 48, p. 368, 1923.

low notch, as shown in figure 29, B. The interclavicle of U.S.N.M. No. 15566 differs in having a V-shaped notch that extends farther posteriorly into the bone. (Compare A and B, fig. 29.) On the ventral surface a sharp median keel develops at the posterior edge of the notch, continuing backward for a short distance before merging into the transversely rounded surface of this side. The posterior fourth of the bar is slightly spatulate in outline, terminating in a bluntly pointed end. Viewed from the side, this bone in front of the cross bar turns strongly upward.

Measurements of interclavicle (in millimeters)

	No. 15559	No. 15568
Greatest length.....	54	55
Greatest width, anterior end.....	9.0	11.5

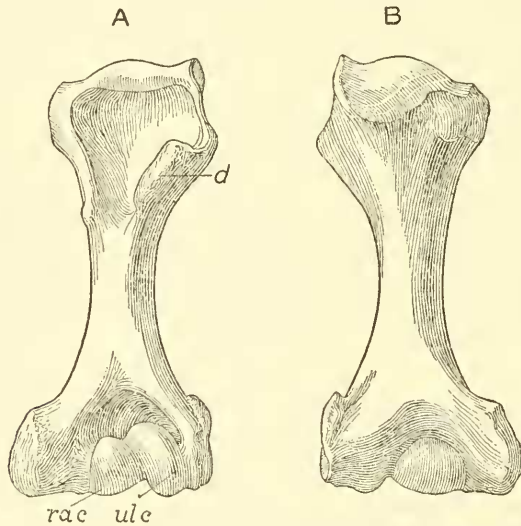


FIGURE 30.—Left humerus of *Polyglyphanodon sternbergi* Gilmore, U.S.N.M., No. 15566, natural size: A, Anterior view; B, posterior view. *d*, Deltoid ridge; *rac*, radial condyle; *ulc*, ulnar condyle.

FORE LIMB

*Humerus*.—In all there are 11 humeri preserved with the several specimens, six of which are nearly perfect. For purposes of illustration and description the left humerus of specimen U.S.N.M. No. 15566 is selected as being the most perfect, as shown in figure 30.

The humerus is of the "old-fashioned" reptilian type, broadly expanded at each extremity and joined by a slender shaft. The planes of the two ends meet each other at a slight angle, that of the proximal turned outward from the horizontal. The ends are more expanded than in either *Iguana* or *Cyclura*, and the shaft is relatively shorter

and stouter. The proximal articular facet, viewed from above, is subovate in transverse outline; its surface is moderately convex in both directions, but more especially anteroposteriorly and extending well backward on the posterior surface, thus indicating a more or less horizontal position of the bone in normal pose. There is a strongly developed deltoid ridge that is extended farther down on the shaft than in any of the *Iguanidae*. On the inner posterior surface near the upper articular end there is a roughened rugosity for muscular attachment. The anterior or ventral surface of this end is deeply concave. The deltoid ridge on the upper third of the bone when in natural pose looks strongly ventral. The articulations for the ulna and radius are turned strongly upward on the anterior surface of the distal end. The larger outer condyle for the ulna rises mostly from the ventral surface, the radial condyle is about subequal on both dorsal and ventral surfaces, as shown in figure 30. On the ventral side above these condyles the bone is excavated by a deep depression, as in *Cyclura*. This depression is only faintly indicated in *Iguana*. In the abrupt inward extension of the radial border the distal end has a decided resemblance to that in *Iguana tuberculata*. The shaft is nearly straight and subovate in cross section.

*Measurements of humerus (in millimeters)*

	No. 15566
Greatest length.....	61
Greatest width of proximal end.....	27
Greatest width of distal end.....	26
Least diameter of shaft.....	6

*Radius and ulna.*—There are seven complete ulnae and the proximal end of an eighth and five perfect radii in the collection, and except for a slight difference in size all are in close agreement. The description is based on the left ulna and radius of U.S.N.M. No. 15559 shown in figure 31.

The radius is a slender bone with subequal expanded ends. Its subovate proximal end is cupped for articulation with the radial condyle of the humerus. The shaft is nearly straight and subround in cross section. The lower distal end is diagonally truncate to the longer axis of the bone (see B, fig. 31), having a slightly cupped articular end.

The ulna is longer than the radius, with a stout olecranon process. Its proximal sigmoid surface is concave and extends upward on the

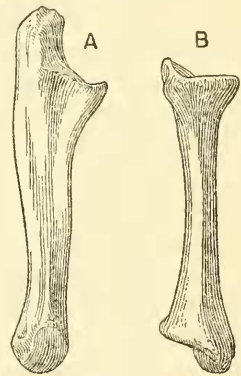


FIGURE 31.—Left radius and ulna of *Polyglyphanodon sternbergi* Gilmore, U.S.N.M. No. 15559, natural size. (A, Ulna, internal side view; B, radius, front view.

anterior face of the olecranon. The radial border of this end is concave. The whole bone tapers from above downward, the shaft is flattened transversely, the least diameter being on the lower third. There is but little expansion of the distal end. The convex articular surface of this end continues upward to an equal extent on both the anterior and posterior aspects. The posterior surface is abruptly backward from the shaft.

Such slight differences as are found in these bones of different individuals can be attributed to post-mortem causes.

*Measurements of radius and ulna (in millimeters)*

	Radius (No. 15559)	Ulna (No. 15559)
Greatest length.....	41.3	48.8
Greatest diameter of proximal end.....	10.0	12.3
Greatest diameter of distal end.....	10.5	7.4
Least diameter of shaft.....	3.6	3.4

*Carpus.*—The complete composition of the carpus of *Polyglyphanodon* is not shown in any of the specimens now available. The left carpus of the paratype, U.S.N.M. No. 15816, is probably the most complete, but in its present condition in the matrix as found it is quite impossible to differentiate fully its several elements. By a study of the carpal bones of all available specimens it has been possible to recognize the more important wrist bones. Specimen U.S.N.M. No. 15566 has the radiale attached to the distal end of the radius, thus definitely identifying this element. The radiale is the second largest bone in the carpus. It is of irregular shape, with a thinned anterior border, becoming thickened posteriorly, but more especially toward the outer end, which projects strongly downward and backward when in articulated position. On the anterior ventral surface at midwidth a distinct flattened facet indicates the point of articulation with centrale 1. External to this facet a notch represents the facets for centrale 2. The ulnare is easily recognized on account of its blocklike form and the fact that it is the largest bone of the carpus. It is assumed that there were five carpalia, but only one, the fifth, U.S.N.M. No. 15816, was found in articulated position. It is a small rounded element. The incomplete carpus outlined in figure 32 was drawn after that of the *Iguana*. The close resemblance of the carpal bones to the homologous elements of the *Iguana* carpus leads to the conclusion that when the complete carpus is known it will be found to resemble closely that of the living form.

*Fore foot.*—The manus is represented by the partially articulated right fore foot of specimen U.S.N.M. No. 15568 and the almost complete articulated left fore foot of the paratype, U.S.N.M. No. 15816, as shown in plate 25. In addition to these two articulated feet, several of the other available specimens had scattered portions of the

fore feet preserved. Unfortunately the most perfect manus is preserved in the matrix, palmar side up, and although it furnishes information as to the digital formula, it contributes but little evidence as to the front view of the hand. That shown in figure 32 is based largely on specimen U.S.N.M. No. 15568.

The metacarpals have about the same proportions as in *Iguana* of similar size. Metacarpal III is longest, II and IV being subequal in length, I being the shortest of the metacarpus.

The hand had the primitive formula 2, 3, 4, 5, and 3. The proximal phalanges of digits II, III, and IV are much shorter than the corresponding bones of the *Iguana* manus, in this respect having a general likeness to the feet of some of the Permian Reptilia. The phalangeals articulate with one another by a tongue and groove, the tongue being on the proximal end. The lower proximal surface extends well back in under the grooved distal end of the next preceding phalangeal. All the digits are clawed. The ungual phalanges are long, slightly curved dorsoventrally, and sharply pointed.

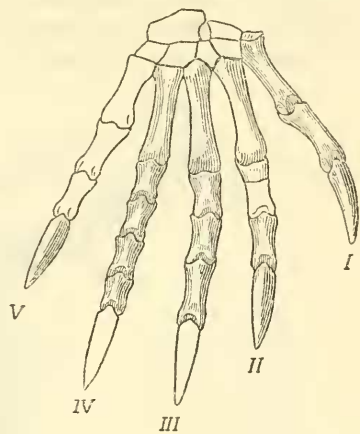


FIGURE 32.—Right fore foot of *Polyglyphanodon sternbergi* Gilmore, U.S.N.M. No. 15568, viewed from the front, natural size: I, II, III, IV, and V, digits 1 to 5, respectively. Digit V has been restored on the evidence furnished by specimen U.S.N.M. No. 15816.

*Measurements of metacarpals of U. S. N. M. No. 15568 (in millimeters)*

Greatest length of metacarpal I.....	10.3
Greatest length of metacarpal II.....	10.4
Greatest length of metacarpal III.....	10.7
Greatest length of metacarpal IV.....	10.3

The pelvis of the type specimen, U.S.N.M. No. 15477, is almost complete, lacking only distal parts of the pubes and a portion of the left ischium. The detailed description is based almost wholly on this specimen. Supplemental materials are the almost perfect pelvises of U.S.N.M. No. 15568 and 15816, in articulated position (see pl. 25), and the left ilium, ischium, and pubis, the last lacking portions of its distal end, of U.S.N.M. No. 15566.

The pelvis as a whole displays no departures from the typical lacertian structure, differing only in certain details from the pelvis of the existing *Iguana*, to which it shows many resemblances.

*Ilium*.—When viewed from the side (see fig. 33) the ilium is produced as a rectangular bar upward and backward from the acetabular

portion. It is of moderate thickness, with a squarely truncated posterior extremity. Near the midlength a swelling outward of the upper and lower borders marks the point of attachment on the inner side of the sacral processes. The rectangular shape of the upper extremity of the ilium presents a marked difference from the tapering

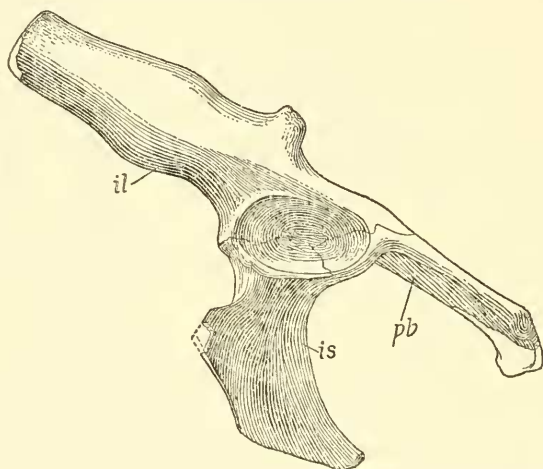


FIGURE 33.—Right half of the pelvis of *Polyglyphanodon sternbergi* Gilmore, U.S.N.M. No. 15477, type, viewed from the right side, natural size: *il*, Ilium; *is*, ischium; *pb*, pubis.

shape of the ilia of *Cyclura* and *Iguana*. On the lower half of the anterior border above the acetabulum, a heavy truncated process projects prominently upward and forward.

At the proximal end the heavy acetabular portion joins the ischium and pubis to form the subovate acetabulum, as shown in figure 33.

*Ischium*.—In articulated position the ischium extends almost directly downward and inward. Below the proximal end, which contributes to the formation of the acetabulum, the shaft is constricted, but it immediately expands into a wide, thin blade that is especially extended anteriorly as a tapering extremity. The distal end meets its fellow of the opposite side on the median line. None of the available specimens shows coalescence along this union, although in aged individuals such a union may be expected. In shape the ischium is iguanid-like in all particulars, resembling *Cyclura* more closely than the ischium of *Iguana*.

*Pubis*.—The pubis extends downward, forward, and inward from the acetabular end, and meets the pubis of the opposite side on the median line by a short symphysis. This inner end, however, is not expanded as in *Cyclura*. The upper posterior border is rounded and thickened from opposite the pubis foramen to the symphysis, forward of which the bone is very thin. Much of this thin portion is missing in all the pubes present, being most complete in specimen U.S.N.M. No. 15816 (see pl. 25). Near the acetabular end the bone is perforated



by the public foramen, which is located near the internal side. Constricted transversely below the acetabular end, the pubis widens rapidly but more especially toward the median line. The outer side is thickened and rounded along the border. The anterior or ventral border is without special thickening and turns inward from the lateral at nearly a right angle.

*Measurements of pelvis of U.S.N.M. No. (15477 (in millimeters)*

Greatest length from upper end of ilium to symphyseal end of pubis-----	83.0
Greatest length of ilium-----	45.7
Width of upper end of ilium-----	10.5
Width of expanded portion of ilium-----	15.0

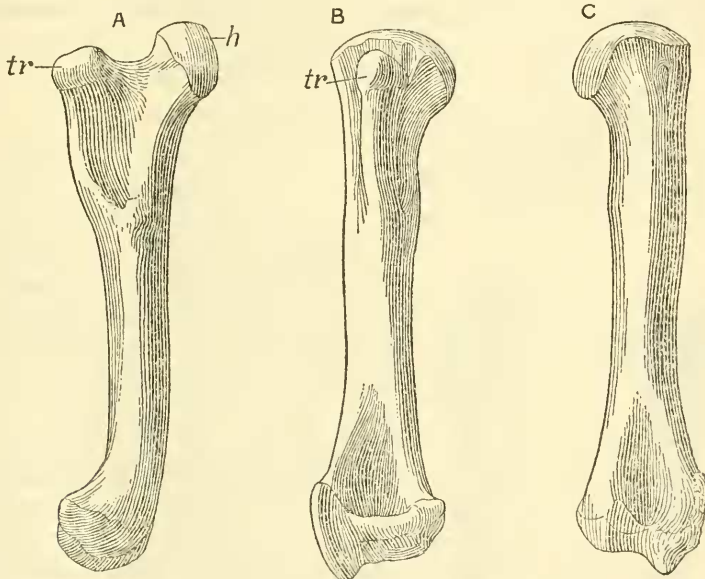


FIGURE 34.—Left femur of *Polyglyphanodon sternbergi* Gilmore, U.S.N.M. No. 15477, type, natural size: A, Inner view; B, posterior view; C, anterior view. *h*, Head; *tr*, trochanter.

HIND LIMB

*Femur*.—In the several specimens of *Polyglyphanodon* available at this time 12 femora are preserved, as follows: two U.S.N.M. No. 15477, the type; two of No. 15816; two of No. 15566; two of No. 15568; one, lacking the proximal end, of No. 15559; two of No. 15817; and one of No. 15819. The description is principally based on the femora of the type specimen, shown in figure 34.

The femur when compared with an *Iguana* of corresponding size is stouter and has heavier articular ends. The great trochanter is robustly developed. It has at its extremity a small ovate facet directed proximally.

Between the trochanter and the head there is a broad shallow fossa that on the inner side extends downward for a distance of about one-

third the length of the bone. In the type femur this fossa has been exaggerated by crushing. The shaft at midlength is nearly circular in cross section, and the bone is nearly straight, except toward the distal end, where it bends backward.

The distal articular surface for the most part looks inward at an angle of about  $30^\circ$  and backward at about  $45^\circ$ . Of the articular surface, that part on the inner side for the tibia is much the broader, being set off from the fibular portion by a projecting ridge or condyle that turns strongly upward on the posterior face. The fibular articulation is principally with the outer side of this condylar projection. The intercondylar fossa is relatively shallow. The epiphyseal suture of the distal end is plainly visible, as shown in figure 34, A.

*Measurements of femur of U.S.N.M. No. 15477 (in millimeters)*

Greatest length.....	72.3
Greatest width of proximal end.....	22.0
Greatest width of distal end.....	17.3
Least diameter of shaft.....	7.7
Transverse diameter of head.....	14.2

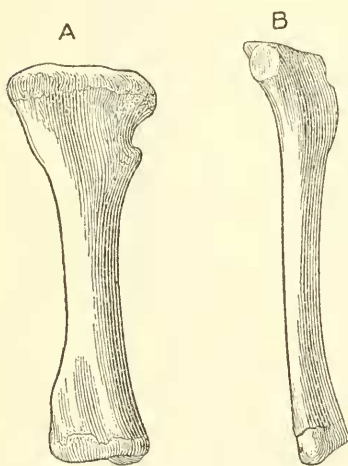


FIGURE 35.—Right tibia and fibula of *Polyglyphanodon sternbergi* Gilmore, U.S.N.M. No. 15477, type, natural size: A, Tibia viewed from the front; B, fibula, lateral view.

*Tibia.*—The tibia is about three-fourths the length of the femur, with a much widened proximal extremity, a stout subovate shaft, and a moderately expanded distal end. In addition to the complete right tibia of the type (see fig. 35), and the distal end of the left, others belonging to seven individuals are in the collections. In the articulated limb the greater diameter of the proximal end is nearly anteroposterior in direction. The cnemial crest is not prominently developed, its outer surface is concave and its inner surface is convex. The condyles of this end overhang the posterior surface of the bone, more especially the outer one. The distal articular end is subovate in outline, with a slightly cupped surface on the outer

half, slightly convex on the inner. The shaft of the bone is practically straight.

*Measurements of right tibia of U.S.N.M. No. 15477 (in millimeters)*

Greatest length.....	52.9
Greatest width of proximal end.....	19.0
Greatest width of distal end.....	13.3
Least diameter of shaft at midlength.....	5.3

*Fibula*.—The fibula, although a slender bone, is stouter than that of an *Iguana* of corresponding size. It is distinctly longer than the tibia, and the planes of the two ends are slightly twisted with respect to one another about the longitudinal axis. Both ends are truncate diagonally to the longer diameter of the shaft. The proximal end is the most expanded, with a swelling out of the anterior border into a thin lip that turns inward. The upper articular surface is long and narrow and turns strongly downward on the inner side for articulation with the condyle of the femur. On the external side at the proximal end a rounded slightly raised projection marks the point of insertion of a ligament (see fig. 35). The distal end is little expanded antero-posteriorly but is thickened transversely. The articular end is convex, the articular surface extending upward on the internal side. In cross section the shaft is subovate in outline.

*Measurements of right fibula of U.S.N.M. No. 15477 (in millimeters)*

Greatest length.....	56.0
Greatest width of proximal end.....	11.7
Greatest width of distal end.....	10.0
Least diameter of shaft at midlength.....	3.4

*Hind foot*.—The structure of the hind foot is best illustrated by the left pes of specimen U.S.N.M. No. 15817, which has every bone present in articulated order, as shown in plate 25. Unfortunately the tarsus can be only partly exposed. This individual is the largest of any of the specimens now available; the femur measures 88 mm. in length as contrasted with 72.3 mm., the length of the femur of the type specimen. The hind foot illustrated in figure 36 is a composite based upon the hind feet of specimen U.S.N.M. No. 15568 preserved in nearly articulated position. Elements that are missing in one foot are usually present in the other, so that by a study of both it has been possible to determine the complete composition of the pes. The correctness of this restoration of the hind foot is now fully verified by the complete left pes of U.S.N.M. No. 15817, shown in plate 25, which came to hand after the drawing had been completed.

Unfortunately both tarsi were in a disturbed state and their complete structure is therefore rendered uncertain, a remark that applies equally well to specimens U.S.N.M. Nos. 15816 and 15817, shown in plate 25. It is for that reason that no attempt has been made to restore the complete tarsus in figure 36 further than illustrating those elements about whose identity there can be no doubt.

The tarsus consists of not less than six, possibly seven, bony elements. The proximal row consisting of the coalesced astragalus and calcaneum. These blocklike bones are so completely fused that their exact line of separation is difficult of detection.

The astragalus or tibiale plus intermedium is subquadrangular in shape when viewed from the front. The tibial articular surface is

subovate in outline and bifossate. The anterior face of this bone is concave with its upper and lower margins raised. The distal end presents a small rounded facet that looks forward and downward, and posterior to it a narrowed articular surface that extends upward on the posterior face for more than half its length.

The calcaneum is smaller than the astragalus, with a cupped articular upper surface for the fibula that is oblique to the longest planes of the

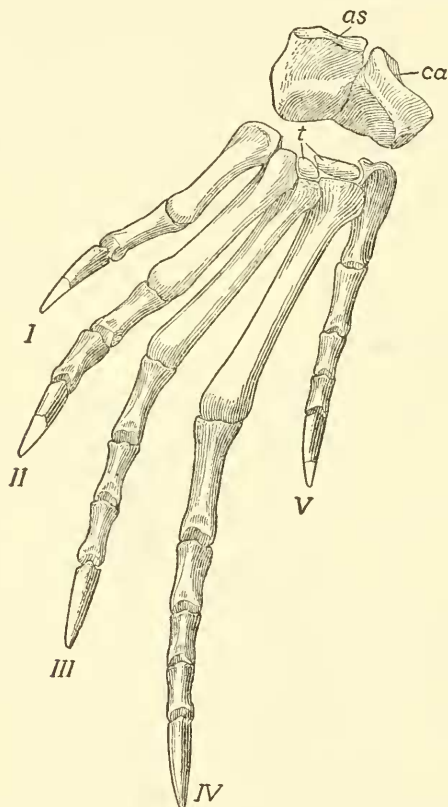


FIGURE 36.—Left hind foot and part of tarsus of *Polyglyptanodon sternbergi* Gilmore, U.S.N.M. No. 15568, natural size, restored from both hind feet [the astragalus and calcaneum (reversed) from type specimen, U.S.N.M. No. 15477]: *as*, Astragalus; *ca*, calcaneum; *t*, tarsalia 3 and 4; I, II, III, IV, and V, digits 1 to 5 respectively.

coalesced bones. The inner ventral surface is recessed by an oblique facet that looks downward and inward; a second smaller facet is present on the extreme outer distal end which probably articulated with tarsale 5. A flattened but irregular shaped element in the articulated right foot at the upper end of metatarsal IV and in articulation with metatarsal V probably represents tarsale 4. A small subtriangular element present in both hind feet at the end of metacarpal III is regarded as tarsale 3. Its position is shown in figure 36.

The five metatarsals increase in length progressively from the first to the fourth, which is the longest of the series. The fifth is the shortest and is further distinguished by the great winglike expansion of its upper end, as in *Iguana* and *Cyclura*. In the articulated foot this expansion of the fifth metatarsal extends inward behind metatarsal IV and articulates along its upper border with the cuboid, little if at all with the calcaneum. The fifth metatarsal is strongly bent, as in the Chelonia. In articulation the other metatarsals are somewhat imbricated, the dorsal margin overlapping the thinner inner side of the next outer bone.

The phalangeal formula is the primitive one of 2, 3, 4, 5, 4. All the digits are terminated by sharp compressed unguals. The metatarsals of U.S.N.M. No. 15568 have the following lengths: I, 18.3 mm.; II, 27.4 mm.; III, 33.5 mm.; IV, 36.0 mm.; V, 13.0 mm.

Insofar as comparison is possible, the tarsus of *Polyglyphanodon* shows the closest resemblances to that of *Iguana*. That remark applies equally well to the foot. The phalangeal formula, the relative length of the phalangeals, and of the digits as a whole, are in almost perfect agreement with the pes of *Iguana*. The only difference worthy of mention is that the individual elements are somewhat stouter than in an *Iguana* of equivalent size.

*Patellar sesamoids*.—A small diamond-shaped ossification attached by matrix to the posterior side of the distal end of the right humerus of specimen U.S.N.M. No. 15816 appears to represent the *patella ulnaris*. Its position *in situ* gives support to such a conclusion, for, as Camp<sup>6</sup> points out, "the patella ulnaris lies in the tendon of insertion of the triceps which rides over the end of the humerus to reach the olecranon."

This sesamoid is partly bony in most of the *Ascalabota* and cartilaginous in most *Autoarchoglossa*. Fürbringer,<sup>7</sup> however, is inclined to place little significance in either its form or distribution in lizards.

The *patella tibialis* is present in three specimens, U.S.N.M. Nos. 15816, 15817, and 15868. This is a small, irregularly shaped, ossicle-like bone that in most instances is attached by matrix to the distal end of the femur. In one instance it was found lying in the matrix between the proximal ends of the tibia and fibula.

A second but smaller ossification attached to the distal end of the right femur of specimen U.S.N.M. No. 15816 may be the fibular interarticular sesamoid, which is sometimes developed in the femoro-

<sup>6</sup> Camp, C. L., Classification of the lizards. Bull. Amer. Mus. Nat. Hist., vol. 48, p. 408, 1923.

<sup>7</sup> Fürbringer, Max, Zur vergleichenden Anatomie des Brustschulterapparates und der Schultermuskeln. Jenaische Zeitschr. Naturw., vol. 34 (new ser., vol. 27), pp. 443-444, 1900.